CARBON ALLOCATION TO ROOT AND SHOOT SYSTEMS OF WOODY PLANTS

Alexander L. Friend[1], Mark D. Coleman[*], and J.G. Isebrands[2]

[1]Department of Forestry
Mississippi State University
P.O. Drawer FR
MSU, MS 39762 USA

[2]USDA Forest Service
North Central Experiment Station
Forestry Sciences Laboratory
P.O. Box 898
Rhinelander. WI 54501 USA

INTRODUCTION

Carbon allocation to roots is of widespread and increasing interest due to a growing appreciation of the importance of root processes to whole-plant physiology and plant productivity. Carbon (C) allocation commonly refers to the distribution of C among plant organs (e.g., leaves, stems, roots); however, the term also applies to functional categories within organs such as defense, injury, repair and storage (Mooney, 1972). It also includes C consumed by roots in maintenance respiration and nutrient uptake (Lambers, 1987). In this paper we will use the terms "C allocation," "C partitioning," and "component biomass accumulation" (i.e., leaf, stem and root biomass) according to the process-based definitions of Dickson (1989). and Isebrands and Dickson (1991). C allocation is the process of distribution of C within the plant to different parts (i.e., source to "sink"). C partitioning is the process of C flow into and among different chemical fractions (i.e., different molecules, different storage and transport pools). Biomass component accumulation is the end product of the process of C accumulation at a specific sink. In the present review, allocation, partitioning and distribution will be relative terms (e.g., percent of total), whereas growth and accumulation will reflect absolute size (e.g., dry weight, moles of C, etc.).

There have been many reviews of C allocation and partitioning in herbaceous and crop plants (Mooney, 1972; Gifford and Evans, 1981; Gifford et al., 1984; Daie, 1985; Cronshaw et al., 1986; Ho, 1988; Stitt and Quick, 1989; Wardlaw, 1990). In addition, numerous reviews that have focused almost exclusively on woody plants (Kozlowski and

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Keller, 1966; Gierum, 1980; Oliveira and Priestley, 1988; Cannell, 1989; Dickson, i989, 1991; Kozlowski, 1992), although there may be little reason to expect that results from woody plants would differ from other plants if plant ontogenetic stages and temporal factors are compared (Dickson, 1991). C allocation has been reviewed in the context of allocation to plant defense (Jones and Coleman, 1991), C storage (Chapin et al., 1990), C "costs" of nutrient and water uptake (Nobel et al., 1992), C fluxes to the rhizosphere (van Veen et al., 1991), C allocation to symbionts (Anderson and Rygiewicz, 1991), C allocation to reproduction (Chairiello and Gulman, 1991), and C allocation at the whole-plant (Ingestad and Agren, 1991) or ecosystem levels (Raich and Nadelhoffer, 1989). In each of the above cases, C allocation is recognized as being plastic and of fundamental importance to plant biology and ecology. Most of these reviews conclude with the message that more experimentation is needed to evaluate the multitude of hypotheses on C allocation in plants-especially in the case of woody plants, where experimentation has numerous logistical constraints.

The objective of this review will be to succintly but comprehensively review and interpret information on C allocation to root and shoot systems of woody plants, with emphasis on plants that have adventitiously generated root systems. In adventitiously rooted plants, C allocation research has been largely focused on two subjects: 1) the effects of carbohydrate storage and allocation of C to stems on rooting and establishment of cuttings, and 2) whether adventitiously rooted plants develop normal root systems, including balanced root/shoot C allocation (see, e.g., the chapter by Dickmann and Hendrick in this volume). Therefore, we will include some information on various subjects that has been obtained with nonadventitiously rooted plants when such information is absent or deficient for adventitiously rooted plants. After a brief introduction, we will explore the controls of C allocation, including plant factors and environmental factors. The plant factors section will include a general discussion of plant controls and root-shoot feedbacks, and will conclude with a discussion of differences between adventitiously rooted plants and those of seed origin, where those differences are known. The environmental factors section will review the influences of nutrients, water, 0, and temperature on C allocation. The final section will be devoted to reviewing and evaluating methods and possible future research directions.

PLANT FACTORS

Intact Plants

General Patterns. In order to understand C allocation in rooted cuttings it is essential to have an appreciation of the general C allocation patterns that occur within intact woody plants. These patterns are highly integrated within the plant and are determined at the early embryonic stages of plant development. Moreover, they are regulated by a complex network of competing sources and "sinks" within plants (Dickson, 1991). Sources are defined as net exporters of photosynthates, and sinks as net importers of photosynthates (Ho, 1988). An interdependency between the shoot and root exists throughout the life of a plant (Kozlowski, 1971), with the feedback between the root and shoot playing an important role in the regulation of overall plant growth and development (Davies and Zhang, 1991).

C allocation patterns are a function of source-sink interactions. The sink-strength within woody plants varies markedly by species, genotype, shoot type, age of plant, location within the plant, season and environmental conditions (Kozlowski, 1992). Although there are exceptions to almost all generalizations made about root-shoot interactions and function (Groff and Kaplan, 1988; see the chapter by Barlow in this volume), there are three fundamental C allocation patterns in woody plants (Dickson, 1991: Kozlowski, 1992). The first pattern is associated with determinate (or fixed) shoot growth, which is characterized by a single, short burst of shoot growth in the late spring and early summer followed by a long lag period of budset. Distribution of assimilates is according to the flush-cycle with most of the assimilates (i.e., > 90%) directed upward to the flush during the flushing episode, and conversely most of the assimilates (i.e., > 95%) are directed downward to the lower stem and roots during the lag stage in between flushing episodes. An example of a genus with this pattern is *Picea.* The second pattern is associated with indeterminate (or free) shoot growth, characterized by continuous shoot growth over most of the growing season. Distribution of assimilate in these plants varies with the stage of development of each leaf. Young developing leaves are net importers of assimilate until they become fully expanded, at which time they export both acropetally to developing leaves and basipetally to the stem and roots. Mature leaves export almost exclusively to the lower stem and roots. An example of a genus exhibiting this pattern is *Populus.* The third pattern is associated with semi-determinate (or recurrent flushing) shoot growth, characterized by periodic flushes of shoot growth with intermediate lag stages. The distribution of assimilate in these plants is cyclic with transport upward to developing leaves during a flush and downward to the stem and toots during the lag; the cycle is repeated during each consecutive flushing episode. An example of a genus with this pattern is *Quercus.*

A common denominator in each of the allocation patterns is the importance of anatomy to understanding C allocation to roots. Specifically, the pathways through which source-sink interactions occur in woody plants are strongly dependent upon the vascular connections delimited during the early primary vascular development of the plants (Larson, 1983). This concept has been supported by Larson and coworkers in a wide variety of plants, including *Populus* (Larson et al., 1980). *Osmunda* (Kuehnert and Larson, 1983), *Gleditsia* (Larson, 1984), *Fraxinus* (Larson, 1985) and *Polyscias* (Larson, 1986).

The overall finding from this review of the literature is that most studies, particularly mechanistic ones, have focused on understanding C allocation to shoots rather than roots. For example, the comprehensive review of C allocation and partitioning by Wardlaw (1990) provides only minimal coverage of allocation to roots. This deficiency is not the fault of the author, but rather a reflection of our current state-of-knowledge on C allocation to roots in plants.

Mechanisms of Carbon Allocation. In order to better understand adventitious rooting in woody plants, it is not enough to know what the patterns of C allocation are in roots and shoots; it is necessary to know how they occur and their significance to plant function. Thus, an understanding of the mechanisms of C allocation and partitioning may facilitate improvements in adventitious rooting (e.g., recalcitrant plants: see Haissig et al., 1992). There have been numerous reviews of the mechanisms of C allocation and partitioning in plants (see Introduction). However, the controlling mechanisms of C allocation remain largely unknown. Some of the genetic, biochemical and physiological aspects of the regulation of transport from sources and sinks are becoming more clear (Cronshaw et al., 1986, p. xxix), yet considerable mechanistic information is still needed. Specifically, two recurring observations are important to understanding adventitious rooting in woody plants.

First, there is increasing evidence that the structural and functional diversity among plants and among tissues within a plant is greater than originally thought. Therefore, the mechanisms controlling C allocation and partitioning during rooting may not be universal and may be specific to species, genotypes and certain tissues (Cronshaw et al., 1986). This means that the specific anatomical differences in rooting between species, which have been shown by Lovell and White (1986), are probably very important in ultimately determining mechanisms and functional properties of rooting of each cutting system; it also means that genetic control is likely to be more important than once thought, as suggested by Haissig et al. (1992). Second, the main control of C allocation between roots and shoots is thought to lie in sink activity (Ho, 1988). Thus, factors affecting sink activity are probably the most important for regulating C allocation and partitioning (Gifford and Evans, 1981). These factors include the biochemistry of sucrose synthesis (Stitt and Quick, 1989; Dickson, 1991). respiration (Gifford, 1986), phloem loading and unloading (Ho, 1988), hormones (Gifford and Evans, 1981). cell turgor (Wyse, 1986) and genetic control (Wyse, 1986). Another important factor is the proximity of the source to the sink and vascular connections between them (Gifford et al., 1984; Dickson, 1989). Indeed, one key to understanding the mechanisms of C allocation in plants lies in understanding the properties of sinks. Important sink-related factors include the initial establishment of the sink at an early developmental stage, duration of sink growth and sink effects on photosynthesis (Gifford and Evans, 1981).

Rooted Cuttings

In this section we will focus on C allocation and partitioning during adventitious rooting of cuttings of woody plants at three plant developmental stages (Love11 and White, 1986): 1) root initiation, (2) root growth and development, and (3) early field performance. Representative sources with the genera studied are presented in Table 1. Readers interested in reviews of the use of carbohydrates during cambial growth of roots, root thickening and mycorrhizae are referred to Kozlowski (1992), and in rootstock C storage to Priestley (1970).

Table 1. List of carbon allocation and partitioning studies conducted on cuttings from woody plants[1].

Genus	Cutting Type[2]	Setting	Reference
Acer	Softwood	Polyhouse	Donnelly (1977)
"	"	Greenhouse	Smalley et al. (1991)
Castanea	Hardwood	"	Vieitez et al. (1980)
Juniperus	"	"	Henry et al. (1992)
Malus	Hardwood	Controlled environment	Cheffins & Howard (1982)
"	Root	Storage	Robinson & Schwabe (1977)
Morus	Softwood	Greenhouse	Satoh et al. (1977)
Pinus	Hardwood	Controlled environment	Cameron & Rook (1974)
"	Softwood	" "	Emstsen & Hansen (1986)
"	Softwood and Seedlings	" "	Haissig (1984)
"	Softwood	" "	Haissig (1989)
"	"	" "	Hansen et al. (1978)
Populus	Softwood	Controlled environment	Dickmann et al. (1975)
"	Root	" "	Eliasson (1968)
"	Hardwood	" "	Fege (1983)
"	"	Storage	Fege & Brown (1984)
"	"	Field	Friend et al. (1991)
"	"	Field	Isebrands & Nelson (1983)
"	"	Outdoor - Pots	Nanda & Anand (1970)
	"	Field	Nelson & Isebrands (1983)
	"	Outdoor - Pots	Nguyen et al. (1990)
	Softwood	Controlled environment	Okoro & Grace (1976)
	Hardwood	Outdoor - Pots	Pregitzer et al. (1990)
	"	Greenhouse	Tschaphnski & Blake (1989)
Olea	Softwood	Greenhouse	Rio et al. (1991)
Prunus	Softwood	Greenhouse	Breen & Muraoka (1974)
Rhododendron		Storage	Davis & Potter (1985)
"		Greenhouse	French (1990)
Triplochiton	"	Greenhouse	*Lcakcy & Coutts (1989)*

[1] Includes only example, primary, English-language references for studies with rooted cuttings; later papers by the same authors may be available. [2] "Softwood" and 'hardwood" as per Dirr and Heuscr (1987).

Root Initiation. Adventitious roots arise either in *situ* as induced root primordia or as preformed root primordia (Haissig, 1974a; Sutton, 1980; see the chapter by Barlow, and by Haissig and Davis in this volume). Thus, there are important anatomical differences among species: those that create a root primordial site and those with sites already present (Love11 and White, 1986). Initiation of adventitious roots is regulated by a balance of internal substances, including carbohydrates, hormones and nitrogenous compounds and, perhaps, related “cofactors” (Kozlowski, 1971; Haissig, 1974b, see also the chapter in this volume by Howard, and by Blakesley). However, genetic control of adventitious rooting is also very important (Haissig, 1986; Haissig, et al. 1992), as evidenced by the wide variation in rooting among closely-related taxa, and by the variety of adventitious root types (Kozlowski, 1992; see the chapter by Barlow in this volume).

Understanding source-sink relations during and subsequent to root initiation depends upon knowledge of anatomical differentiation (Haissig, 1986). Success or failure of rooting depends upon the establishment of a vascular link between source and the new sink (i.e., root). This linkage (or lack thereof) has been hypothesized to be dependent on anatomical characteristics of the cutting (Vieitez, 1974; Vieitez et al., 1980) and is related to presence of secondary development associated with maturation and aging. A common element among some species that have preformed root initials and those that form roots *in situ* is the association of the new root (i.e., sink) in close proximity to existing vascular tissue (i.e., source). For example, in *Salix*, preformed root initials occur in leaf gaps of nodes next to vascular traces, as described by Haissig (1970). In *Quercus rubra*, a recalcitrant semideterminate species, adventitious roots form *in situ* in vertical rows in association with stem vascular traces (Isebrands and Crow, 1985).

Knowledge of source-sink relations between roots and shoots of intact plants may add to our understanding of C allocation in rooted cuttings. For example, in the nodal region of *Populus*, Isebrands and Larson (1977) found that there are two significant attributes of cambial development in vascular bundles within leaf gaps: 1) fusion of cambial initials between adjacent vascular bundles occurs when a critical minimum tangential distance is attained, and 2) cambial initials within bundles exhibit polarity with respect to adjacent bundles. Similar phenomena occur during the linkage of differentiating cells in tissue cultures of Coleus and *Daucus* (Lang, 1974). during differentiation of vascular bundles of secondary veins in *Populus* leaves (Isebrands and Larson, 1980), and in the vascular union between developing axillary buds (i.e., branches) and the stem in *Populus* (Larson and Fisher, 1983). If the analogy extends to adventitious roots, these phenomena may explain the ease of rooting cuttings in species with preformed root initials in leaf gaps. In those cases, root cambial cells are in close proximity to cambial cells of adjacent leaf traces and in a favorable position to establish the early vascular connections between the source and sink that are necessary to provide carbohydrates and hormones required for the formation of roots. Another example is the establishment of the vascular system in new germinants from *Populus* seed (Larson, 1979). In the early stages of seedling development, the procambium differentiates in ground tissue in the region of the prospective hypocotyl (root), and develops acropetally and continuously with the epicotyl (shoot). Thus, a procambial template system is formed between root and shoot that determines all subsequent vascularization of the plant. Early vascularization of the seedling, determined by phyllotaxy, is thereby responsible for integrating structural-functional relationships of the whole plant. Similar structural-functional relationships have been found in the early vascularization of the root and shoot in sugar beet (Stieber and Beringer, 1984). Therefore, successful functioning of plants developing from seed depends upon the intimate structural-functional connection between the shoot (source) and root (sink), just as in rooted cuttings.

Haissig (1986) presented a comprehensive review of C metabolism of cuttings during root initiation. Although carbohydrates are considered the principal source of energy during rooting, there is substantial variation in the use of carbohydrates among species and cutting types. There is considerable controversy over the role of carbohydrates during rooting due to differences in environment, experimental approaches and interpretation by researchers (Haissig, 1986). Stockplant factors are also known to be important in determining carbohydrate status in cuttings (Hansen et al., 1978; Emstsen and Hansen, 1986; Leakey and Coutts, 198% see also the chapter by Howard in this volume). Therefore, it is difficult to use one measure of carbohydrates as an independent variable for predicting rooting success. Nevertheless, some examples of carbohydrate dynamics associated with adventitious rooting will be presented below.

Total carbohydrates of cuttings are thought to be related to rooting, but not necessarily causally (see the chapter by Haissig and Davis in this volume). For example, Fege and Brown (1984) found that total carbohydrates were greatest in large-diameter *Populus* hardwood cuttings and were correlated with rooting success, but concluded that other factors may be more important than carbohydrate content for rooting success. Breen and Muraoka (1974) found that most ^{14}C transported from leaves (after a $^{14}CO_2$ pulse) of softwood cuttings of *Prunus* remained in the upper stem until rooting commenced, at which time a four-fold increase in ^{14}C concentration occurred at the cutting base. However, they concluded that an unspecified root promoting substance was probably more important than carbohydrate content for successful rooting. Haissig (1984) studied carbohydrate concentrations *in Pinus banksiana* stem cuttings, and found that total carbohydrate accumulation was correlated with basal stem callus rooting; again, no causal relationship was established. Moreover, he found that differential partitioning of carbohydrates, specifically, the ratio of reducing sugar to starch, was a good indication of rooting success. In a recent review, Veierskov (1988), concluded that an abundance of stored carbohydrates Will improve the success of rooting if other physiological conditions are favorable. However, the physiological state of the plant may have an overriding influence and result in poor rooting even in plants with high carbohydrate concentrations. Clearly, several factors are important in determining the role of carbohydrates in root initiation: origin of roots (callus or preformed initials), types and availabilities of carbohydrates, autocorrelations between carbohydrate accumulations in cuttings and other growth-affecting chemicals, genetic variation in optimal carbohydrate balance for rooting, phenological stage, and other plant factors. In summary, more research is needed which incorporates the plant factors mentioned above (Haissig, 1986; Haissig et al., 1992).

Root Growth and Development. Although there has been much research on C allocation and partitioning at the initiation stage of adventitious rooting of woody plants, there are far fewer studies during the “early” stages of root growth and development. This paucity of research seems to be related to the lack of suitable methods and approaches for studying cuttings during the transition between root initiation and root growth. Carbohydrate reserves are very important during root initiation, while subsequent growth may be almost entirely dependent on current photosynthate. Haissig (1988) has suggested that radiotracers offer the most suitable techniques for studying these processes and has called for a multidisciplinary use of radiotracers to improve our understanding of C metabolism during the various stages of adventitious rooting. However, despite the availability of simple and inexpensive radiotracer methods (Isebrands and Dickson, 1991; Isebrands and Fege, 1993), few investigators have used them.

As an exception, early C allocation patterns in softwood cuttings were investigated by Breen and Muraoka (1974) using leafy softwood cuttings exposed to $^{14}CO_2$ to study the changes in carbohydrate content in softwood cuttings of *Prunus* during and after root initiation. They showed that the proportion of ^{14}C increased at the stem base after root initiation. They also found a decline in ^{14}C in sugar over time, indicating a metabolism of carbohydrate reserves in the cutting during rooting. After labeling, the percentage of total ^{14}C in reserves declined in the cutting base from 80% at the start to nearly 20% at day 28 of the chase period, while the residue fraction (i.e., structural carbohydrates) increased during the chase period mostly in cuttings with a good rooting percentage. Another study of ^{14}C allocation found that 75% of the photosynthate transported to developing roots of *Pinus radiata* softwood cuttings came from the older. mature foliage when compared with the younger, recently expanded foliage (Cameron and Rook, 1974). Results from both of these studies indicate that source-sink relations of foliage and roots are very important in affecting the allocation of C to developing roots in softwood cuttings.

The role of stored assimilates during adventitious root formation and subsequent growth after outplanting in the field was examined by Isebrands and Fege (unpublished) using hardwood cuttings of *Populus* in Wisconsin. They labelled coppice sprouts *in vivo*, harvested radiolabelled hardwood cuttings during the winter, then followed ^{14}C in the cuttings during early root development. Carbohydrate reserves played an important role in the growth of developing leaves during the first four weeks before any root growth occurred. After that time, current photosynthate was more important for subsequent leaf and stem growth. Root growth used stored photosynthate for a longer period than above-ground components (i.e., ca. six weeks after planting), thereby following the leaves and stem in dependence upon current photosynthate.

Some researchers have used biochemical methods other than radiotracers to study the early root growth and development phase of rooted cuttings. Okoro and Grace (1976) studied carbohydrate concentrations of leafless hardwood cuttings and softwood cuttings of various *Populus* species. In the leafless hardwood cuttings, concentrations of carbohydrates were initially high and fell rapidly as roots developed. However, even at the final stages of the experiment, much reserve carbohydrate remained. Leafy softwood cuttings had a different pattern in that they exhibited a steady accumulation of carbohydrate from the time of planting to the time that roots developed. The authors noted that root production in both hardwood and softwood cuttings extended leaf longevity on the cutting and increased leaf photosynthesis, confirming a positive feedback from developing roots to the developing shoot, as in conifer seedlings (van den Driessche, 1987). Using biochemical methods, Tschaplinski and Blake (1989) also studied carbohydrate metabolism in relation to subsequent growth from leafless hardwood cuttings in five *Populus* hybrid clones exhibiting a range of rooting patterns. Their carbohydrate analysis indicated that differences among early clonal performance were related to carbohydrate utilization. Glucose and myo-inositol levels declined more rapidly in faster-growing hybrid clones than in slower ones. They concluded that the faster-growing hybrids consumed the monosaccharide carbohydrates for early growth, while slower growers converted monosaccharides to storage carbohydrates. Myo-inositol concentrations were highly correlated with root growth, although starch was not. These results prompted the authors to recommend myo-inositol concentration as a possible early selection index for early root production in hardwood cuttings of poplar.

Field Performance. The number of C allocation and partitioning studies in woody plants reared from cuttings and grown under field conditions is limited. This general lack of information on field-based C physiology (Isebrands and Dickson, 1991) is somewhat surprising, considering the recently expanded commercial use of cuttings in forestry (Ritchie, 1991; see the chapter by Ritchie in this volume) and their long-standing use in ornamental horticulture (see the chapter by Davies and coworkers in this volume). Much of the existing work to date has been part of research programs focused on developing short- rotation woody crops for biomass and energy (Isebrands et al., 1983; Stettler et al., 1988). Moreover, much of the research has been with *Populus* because that genus exhibits outstanding biomass production under a short-rotation system (Hinckley et al., 1989). C physiology studies on horticultural trees have largely been on plants derived from rootstocks, not hardwood cuttings (Priestley, 1970).

Isebrands and Nelson (1983) studied C allocation patterns in the establishment year in two intensively cultured ***Popufus*** clones with contrasting phenology and morphology; plants were grown in the field from hardwood cuttings. Using radiotracers, they found clonal differences in seasonal patterns of C allocation that were related to phenology. The timing of budset was the most important factor in determining allocation differences between the clones. Prior to budset, export was primarily upward to developing leaves. Following budset, mature leaf export was primarily to the lower stem, hardwood cutting and roots. Moreover, one of the clones, 'Tristis,' exported a greater proportion of carbohydrate to roots, suggesting that the sink strength of roots in *Populus* is under genetic control (see the chapter by Dickmann and Hendrick in this volume). As the season progressed, lower leaves were the primary source of photosynthates for root growth. The C allocation patterns were largely consistent with the general patterns characteristic of indeterminate woody plant seedlings (Dickson, 1986). In a companion study with a clone that exhibited late-season leaf retention, it was concluded that autumnal retention of leaves is important for root growth and the accumulation of reserve storage in the cutting and roots (Nelson and Isebrands, 1983).

Although relatively little is known about the role of hardwood cuttings in C allocation during years subsequent to establishment (Isebrands et al., 1983; Dickson, 1986). some information exists. We have used ^{14}C methods to study C allocation of *Populus* clones in the second year in the field, from hardwood cuttings (Friend et al., 1991). In that study, the hardwood cutting itself grew considerably in size from the time of planting through the second season when it became fully incorporated in the stem-root transition (see the chapter by Dickmann and Hendrick in this volume). C allocation to below-ground biomass components was evenly distributed among the cutting, coarse roots and fine roots, indicating that the cutting is still an active sink for photosynthate beyond root initiation stages and into the second growing season.

Hinckley et al. (1989) reviewed C allocation patterns during the first and second year of four hybrid poplar clones grown from hardwood cuttings in Washington state in a study conducted by Scarascia-Mugnozza (1991). They found a progressive shift of photosynthate allocation from the upper leaves and stem to the lower stem and roots as the season progressed. Clonal differences were observed in allocation to roots, with one clone (i.e., H44-136) maintaining a high allocation to the cutting, coarse roots and fine roots throughout the entire growth period. Clones also varied in the number, size and orientation of roots as they developed. It was concluded that high allocation to roots in the first year resulted in greater productivity of the clone in the second year. Similar studies have been conducted by Pregitzer et al. (1990) and Nguyen et al. (1990).

Root-Shoot Feedback

Within higher plants the specialized functioning of photosynthetic energy fixation in leaves must be coordinated with nutrient and water absorption of roots. The coordination between plant roots and shoots is apparent when considering the dynamic responses of root-shoot C allocation to environmental factors. Early establishment of root-shoot balance is especially important for rooted cuttings. Without an adequate root system to balance the existing shoot, normal plant development is not possible. A number of proposed mechanisms account for the coordination of specialized functions among the various plant organs, including resource-based functional equilibrium, metabolic control and chemical signals such as phytohormones or metabolites. These possible mechanisms for coordination of C allocation will be discussed below.

Functional Equilibrium. Brouwer (1983) emphasized that the dynamics of root-shoot interactions are dependent upon a functional equilibrium between root and shoot. Under certain environmental conditions, plants will adjust relative growth to maintain a constant root:shoot biomass ratio, even if roots or shoots are partially abscised. Further, if the ability of one organ to supply C or mineral nutrient resources is disturbed through changing environmental conditions, it will affect the growth and functioning of other dependent organs, resulting in a new equilibrium (Brouwer, 1983). Because the dynamics of functional equilibrium are exhibited by many plant species and influenced by a variety of environmental conditions, the idea of growth regulation, through supply of and demand for internal resources, continues to be viewed favorably (Dickson and Isebrands, 1991; Klepper, 1991). Bloom et al. (1985) postulated that the cost for resource acquisition, in terms of reserve C and nutrient resources used, could be weighed against the gain of having obtained such resources. Further, and in line with functional equilibrium, they speculated that plants can adjust internal supply of and "demand" for resources by allocating internal reserves and adjusting growth patterns.

The relationship between root-shoot equilibrium and internal resource balance is most apparent when considering the balance between C and nitrogen (N). Internal N concentration is strongly related to C allocation processes (Rufty et al., 1988) and root:shoot ratio (Agren and Ingestad, 1987). The correlation of root-shoot allocation with N supply is controlled by internal non-structural C to N (C:N) concentration ratios (Brouwer, 1983; Mooney and Winner, 1991). Mooney and Winner (1991) considered the C:N ratio to be at some "set-point" value which, if disturbed, would adjust root or shoot growth and activity. The C:N ratio set-point would then be reestablished. Once the C:N set-point was reestablished. a new root:shoot ratio would be achieved. Such an approach has resulted in relatively accurate predictions of root-shoot balance based on C:N ratios in simulation models (Thomley, 1972; Reynolds and Thomley, 1982). However, the failure of these models to maintain equilibrium conditions without prescribing specific C:N ratios suggests that some other control factors may be involved. Nevertheless, similar C:N set-points may be useful constructs in which to investigate the optimum carbohydrate storage that maximizes rooting of cuttings (cf. Leakey and Storeton-West, 1992).

Metabolic Control. The correlative relationship between root-shoot C allocation processes and C:N ratios suggests the importance of C and N metabolism to understanding these processes. For example, Huber (1983) examined a variety of species under various light and N treatment conditions, and concluded that root:shoot ratio is inversely related to accumulation of leaf starch. Leaf starch accumulation and sucrose formation are regulated by sucrose phosphate synthetase (SPS) (Huber et al., 1985). Because SPS activity affects the supply of sucrose for export (Kerr et al., 1983; Huber et al., 1985), a possible link between leaf carbohydrate metabolism and control of root-shoot C allocation is apparent. Regulation of enzymes known to be responsible for the partitioning between starch and sucrose, including SPS, has been extensively studied (Stitt et al., 1987; Stitt and Quick, 1989; Stitt, 1990; Huber and Huber, 1992). On the basis of this work, it is evident that a number of factors that affect C allocation to the root and shoot also affect the partitioning between starch and sucrose. For example, it is possible that the interdependence of carbohydrate metabolism and nitrate reduction in leaves (Huber and Huber 1992) is an important regulating point for C allocation processes. In this case, the N moving in the vascular system may act as a controlling factor over C allocation processes.

Nitrogenous compounds are known to move not only from root to shoot in the xylem but also in the phloem (Lambers et al., 1982; Patrick, 1988), especially under nutrient-stress conditions where shoot activity is minimal. In addition, roots growing in N-rich soil patches tend to show greater growth and respiration rates, as well as nitrate reductase activity (Lambers et al., 1982; Lambers, 1987; Granato and Raper, 1989), all of which increase the demand for carbohydrate and the amount translocated to roots (Patrick, 1988). In this way, vascular transport of nitrogenous compounds, N uptake and N metabolism in roots may have considerable control over C allocation.

Phytohormones. Plant hormones and other metabolically active compounds moving up from roots to leaves in xylem or down to roots from leaves in phloem have long been considered strong influences in root-shoot interactions (Skene, 1975). There is little doubt that signals coming from herbivore-damaged tissue are responsible for initiating gene transcription in remote locations (Ryan and Farmer, 1991). Abscisic acid (ABA) signals moving in the xylem sap clearly demonstrate that root-shoot interactions occur via hormones. Soil-drying experiments are known to affect leaf conductance and growth before affecting turgor (Davies and Zhang, 1991), and exogenous leaf application of ABA will reduce leaf conductance (Mansfield, 1987).

Hormones may also influence C allocation processes. It is known that the enzymes responsible for regulation of starch-sucrose partitioning are influenced by plant hormones (Daie, 1986; Cheikh and Brenner, 1992). Growth of roots is favored over the growth of shoots following exogenous application of ABA, and this response is similar to the effects of water-stress treatments (Watts et al., 1981). The negative effect of root or shoot excision on sucrose translocation toward that organ can be reversed by application of auxin or cytokinin to the site of the removed organ (Gersani et al., 1980). Dependence of shoot growth on root-supplied hormones is considered to be most important under conditions of limiting nutrients. Therefore, it may be that hormonal control is less important under greenhouse than field conditions where nutrients are often limiting (Wareing, 1980).

While a number of processes are affected by phytohormones, there is little consensus among physiologists that hormonal control is necessary to maintain root-shoot equilibrium. Although it is likely that plant hormones and other metabolically active compounds are participating in the fine control of feedback between roots and shoots, their role is unclear (Patrick, 1987). When considering this point, and the effective coarse-control of functional equilibrium to describe C allocation, it is understandable that researchers have not incorporated the fine control of hormones in simulation models (cf. de Wit and Penning de Vries, 1983; Wilson, 1988).

Comparison of Adventitiously Rooted Plants and Seedlings

There has been considerable research on the field performance of adventitiously rooted plants compared with seedlings, but only a few studies have investigated differences in C allocation between vegetative propagules and seedlings. One of these is the work of Haissig (1984) who compared carbohydrate accumulation and partitioning in *Pinus banksiana* seedlings and cuttings during root initiation. He found differences between the two in the amount of individual carbohydrates accumulated and in the location of accumulation. All parts of cuttings accumulated more carbohydrates when compared with seedlings. The most pronounced difference between cuttings and seedlings was in the reducing sugar:starch ratio, which was much lower in cuttings than in seedlings. Studies of *Populus* hybrids have found one distinct difference between hardwood cutting-derived plants and seedlings: the hardwood cutting is a relatively large and active sink for photosynthate compared with the stem of a seedling of similar size (Isebrands and Nelson 1983). In fact, large quantities (i.e., 20 to 30%) of ^{14}C-labelled photosynthate from mature leaves were actively incorporated into storage products and cambial derivatives in the cutting during the entire establishment year (Isebrands and Nelson, 1983). These findings are corroborated by the recent work of Scarascia-Mugnozza (1991), which indicates that the cutting is more than simply a conduit for carbohydrates and hormone transport from shoot to root, but instead plays a key role beyond root initiation in the integrated anatomical and physiological development during establishment and subsequent growth of plants from hardwood cuttings in the field. In contrast, recent work with softwood cuttings of *Populus tremuloides* has found no appreciable difference in root-shoot biomass components in response to stress treatments between cuttings and seedlings subjected to ozone-stress (Coleman and Isebrands, unpublished).

After root initiation, the ability to maintain a balance between root and shoot C allocation. and to produce an effective root system, will determine the success of vegetative propagules. Numerous studies have investigated the field performance of plantlets relative to seedlings (Gupta et al., 1991), but few have attempted to link the success, or lack thereof, to C allocation or root-shoot balance. Most effort in this area has been with coniferous tree species, which are of great economic importance but notoriously difficult to propagate vegetatively. For example, in *Pinus taeda*, allometric relations between root and shoot dry weight (DW) do not appear to differ between plantlets and seedlings. However, adventitiously generated plantlet roots are less effective at nutrient uptake due to inadequate branching and large diameters, compared with roots of seedling origin (McKeand and Allen, 1984). Later research with *Pinus taeda*, propagated in a similar manner, confirms these findings and even quantifies the negative impact of this less effective root system on field performance of young plantations (Anderson et al., 1992). This work also noted that a larger part of the early lag in growth of plantlets compared with seedlings is attributable to shoot rather than root effects. Specifically, Anderson et al. (1992) observed a mature shoot morphology in plantlets and provided evidence that this was caused by the shoot rather than factors associated with the adventitious roots. In contrast, work with *Betula* found tissue culture plantlets showed more juvenile shoot morphological traits when compared with rooted cuttings (Brand and Lineberger, 1992). In the above cases, the juvenility or maturity of the roots was not discussed, but presumably roots also have juvenile and mature characteristics, although this phenomenon is less well characterized in roots than in shoots.

Field plantings of *Pseudotsuga menziesii* have been similarly limited by survival, growth and stem form of adventitiously rooted plants compared with seedings (Ritchie and Long, 1986). In contrast to *Pinus taeda*, relative root biomass (root:shoot ratio) is reported to be greater in rooted cuttings than in seedlings of *P. menziesii* (Ritchie et al., 1992). Also, it has been hypothesized that plagiotropism is caused, in part, by abnormal root development (Timmis et al., 1992). Specifically, it is reasoned that the observed asymmetric development of adventitious roots (i.e., on only one side of the cutting) may cause an imbalance in plant growth substances of root origin and provide an erroneous message to the shoot apical meristem. In contrast, mature shoot characteristics of *Pinus taeda* were associated with signals from the shoot and not the root system (Anderson et al., 1992).

ENVIRONMENTAL FACTORS

The ability of plants to adjust C allocation in response to environmental changes is widely documented. While the role of these changes in environmental stress tolerance or acclimation may be debated, many environmentally-induced changes in C allocation are well established. These will be reviewed in the section below, where the information will apply to intact plants and maybe comparable to the responses of stock plants from which softwood or hardwood cuttings might be taken. In addition to the information on intact plants, the C allocation of cuttings in response to environmental factors will be included. The hypothesis that environmental responses of C allocation to adventitious rooting will not differ from that of intact plants will also be examined.

Nutrients

It has been widely stated that the general influence of nutrient-stress on C allocation is to increase C allocation to the roots compared with that allocated to the shoot. This change would seem both intuitive and adaptive because increased root development should, in part, compensate for a nutrient deficiency by increasing the nutrient absorption capacity of the plant. However, this hypothesis has not been rigorously tested until recently. Evidence will be provided from both ^{14}C tracer studies and whole-plant growth analyses.

Although nutrient uptake and metabolism are acknowledged to increase root C consumption (Lambers, 1987; Patrick, 1988), net allocation of ^{14}C to roots has been found to decrease with improved nutrient availability for *P. menziesii* (Friend, 1988). One cause of this pattern appears to be a shift in C partitioning from carbohydrates toward nitrogenous compounds (cf. Marx et al., 1977, Margolis and Waring 1986). Another cause appears to be an increased sink strength of actively growing foliage (high N), which consumes a disproportionate amount of C compared with low N conditions. In a study by Friend (1988) of four-month-old ***P. menziesii*** seedlings, net ^{14}C allocation patterns (CA, Fig. 1) were caused by N effects on both growth of tissues (i.e., sink size; see DW, Fig. 1) and on ^{14}C accumulation rate on a per-unit-tissue basis (i.e., unloading rate or sink activity; see SA, Fig. 1). In this and other studies, trends in DW distribution are usually representative of net C allocation patterns, but caution must be used in drawing inferences about C allocation from analyses of DW, especially given the seasonal variations in C storage common in woody plants and the importance of carbohydrate storage to adventitious rooting.

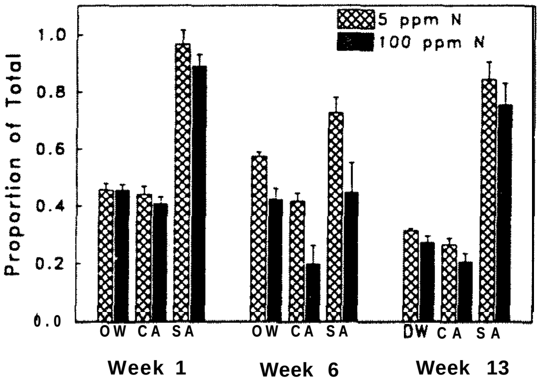

Figure 1. Three measures of carbon allocation to roots in response to nitrogen (N). Four-month-old *Pseudotsuga menziesii* seedlings grown in silica sand with N-deficient (5 ppm N as NH_4NO_3) or N-sufficient (100 ppm N as NH_4NO_3) nutrient solutions added thrice per week. Bars represent paired comparisons between 5 ppm N and 100 ppm N for relative dry weight accumulation (DW; proportion of total), net carbon allocation (CA, proponion of recovered ^{14}C in roots), and relative specific activity [SA; as defined by Mor and Halevy (1979)] at one, six and 13 weeks after treatment. Error bars depict one standard error of the mean. [after Friend (1988)]

One of the best illustrations of nutritional effects on root-shoot development at the whole-plant level is from Ingestad and Agren (1991), who support the hypothesis that nutrient-stress increases root development by showing increased proportions of dry matter in roots compared with shoots as a steady-state nutritional regime is decreased from the optimum. However, their results indicate that this phenomenon cannot be generalized to all nutrients. For example, potassium (K) appears to have no effect on root-shoot biomass distribution, while N, phosphorus (P) and sulfur (S) deficiencies each increase the proportion of biomass in the root system (Ingestad and Agren, 1991). An important additional finding from the use of steady-state nutrition techniques is that the shift in root-shoot biomass distribution occurs over a relatively short time period; subsequently, the relative growth rates of roots and shoots are equal (Ingestad and Lund, 1979). This single, rapid adjustment may apply to steady state conditions only, while a nutrient deficiency under temporally variable field conditions may result in numerous such periods of roof-shoot adjustment, due to short-term fluctuations in nutrient availability.

The increase in root-shoot biomass ratio brought about by nutrient-stress may be caused by either an increase in root growth or by a larger decrease in shoot growth than in root growth. Studies of seedlings commonly report the latter pattern (change in relative not absolute growth). For example, N-stress increased root:shoot ratio in ***P. menziesii*** seedlings primarily through a more negative effect on foliage and stem growth than on root growth (Fig. 2) (Friend et al., 1990). From this and other related seedling studies (Squire et al., 1987; Johnson, 1990), the N-stress effect on root:shoot ratio may be viewed as caused by foliage and shoot growth being more sensitive to and limited by N than root growth. In contrast with seedlings, studies of mature trees indicate that older, larger plants may accomplish a similar shift in root-shoot biomass distribution by different mechanisms. For example, Cower et al. (1992) found that N fertilization of ***P. menziesii*** forests resulted in absolute decreases in fine mot productivity.

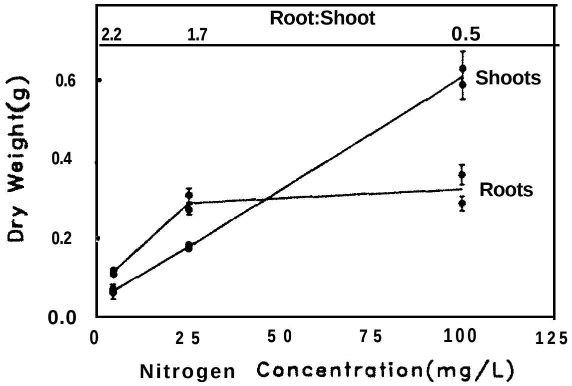

Figure 2. Response of shoot growth. root growth and root:shoot ratio to nitrogen (N) stress. *Pseudotsuga mentiesii* seedlings were grown from seed at a 2.5 cm x 2.5 cm spacing in boxes of silica sand for four months. Weekly, they received a complete and optimum nutrient solution with the exception of N, which was supplied at 5, 25 or 100 mg L^{-1} as NH_4NO_3. Each symbol represents the mean dry weight of the 25 seedlings in each box; error bars represent ± one S.E. of the mean. [Friend and Coleman, unpublished]

Nutrient-stress does not always result in shifts in biomass distribution to roots. Substantial nutrient-induced growth reductions are commonly required before such shifts are evident (Dewald et al., 1992). An additional source of uncertainty is the change in root:shoot ratio that occurs as a function of plant size rather than nutrient addition ***per se*** (cf. Carlson and Preisig, 1981). These uncertainties about nutrient-stress and DW accumulation may have fueled previous skepticism about the nutrient-stress-induced shift in root-shoot biomass distribution (e.g., Carlson and Preisig, 1981).

Mosr of the studies of C:N ratios and adventitious rooting have been oriented toward C partitioning, given the potential role of carbohydrate storage in promotion of rooting. Under conditions of high irradiance, addition of N to stock plants may improve rooting of associated cuttings (Henry et al., 1992; Leakey and Storeton-West, 1992). This response is not always positive, however. The rooting of *Juniperus* declined as N levels added to the stock plant approached optimum for whole-plant growth (Henry et al. 1992) and, at low irradiance, NPK addition to ***Tripfochiron*** stock plants had a negative effect on rooting. In both studies, sugars were better correlated with rooting than was N, but with opposite effects. Specifically, rooting of *Juniperus* cuttings was positively correlated with sucrose content, while that of *Triplochiton* was negatively associated with reflux-soluble carbohydrates. Of additional interest was the very strong correlation between K and boron (B) concentration at the time of excision and the percent rooting of *Juniperus* cuttings (Henry et al., 1992). Collectively, these findings suggest two important differences between the response of root development in intact plants (stock plants) to nutrients and the rooting response of cuttings collected from intact plants. First, severe N-stress increases the root-shoot biomass ratio of intact plants but may not encourage rooting of cuttings. Second, K and B may encourage rooting of cuttings but do not appear to affect biomass distribution between roots and shoots of intact plants.

Water

Water plays a fundamental solute role in the translocation of sucrose from source to sink, in "pressure flow" and in root-shoot "communication." A water deficiency has a cascade of effects on C allocation and partitioning, from those that occur over seconds/minutes to those that occur over days/weeks [reviewed by Geiger and Servaites (199 1)]. Fundamental effects of water-stress include an increased C partitioning to osmotica (Geiger and Serviates, 1991) and altered source-sink relations. For example, water-stress caused decreased export rates of ^{11}C from the source leaf and decreased ^{11}C import rates to sink leaves and roots, relative to unstressed conditions. However, root import under water-stress was decreased less than leaf import (Schurr and Jahnke, 1991). resulting in "relative increase in C allocation to roots. Similar results have been reported for ***Theobroma*** but the change from unstressed conditions was not continuous: net ^{14}C allocation to roots decreased at moderate water-stress before it increased to above-control levels at severe water-stress (Deng et al., 1990). In the same study, the relative accumulation of biomass in roots responded differently than that of ^{14}C because relative root biomass decreased continuously with increasing water-stress. This emphasizes the potential differences between C allocation and DW distribution. In general, however, the proportion of C disuibuted to roots increases with increasing water-stress, as with nutrient-stress, but the absolute amount does not. As a result, root systems under water-stress increase in size compared to the shoot.

The effects of water-stress and nutrient stress on root-shoot biomass distribution are related in two important ways. The first is a similarity: the general effect of both is to increase the proportion of biomass accumulated in roots. However, this increase is caused by a different mechanism in water-stress than nutrient-stress. Water-stress promotes root development because root growth can be maintained at soil water potentials that slow or stop foliage growth (Sharpe and Davies, 1979). In drying soil, roots are able to maintain a greater turgor pressure than foliage and thus continue to grow (Kozlowski et al., 1991, p. 253). The ability of net photosynthesis to continue under water-stress conditions that stop or substantially reduce leaf growth (Kozlowski et al., 1991, p. 265) also contributes to the water-stress-induced increase in root growth; C fixed under these conditions is allocated to roots. In contrast, nutrient-stress effects on root biomass accumulation appear to be caused by inadequate substrate availability for shoot growth, resulting in C accumulation in the roots, which require a lower nutrient supply for growth. The second water- and nutrient-stress relation is an interaction: the effects of drought and water-stress may cause changes in C allocation through the negative indirect effects of water availability on plant nutrient availability. Such indirect effects include the negative effects of dry soil on nutrient release from organic matter (Alexander, 1977, p. 137) and the reduction of ionic mass flow and diffusion through the soil to the root surface (Mengel and Kirkby, 1982, p. 69).

Several experimental studies have investigated the influence of water and nutrients on biomass distribution between roots and shoots with combined irrigation-fenilization experiments (Table 2). Results from these experiments indicate that the effect of nutrient-stress is stronger and more consistent than that of water-stress on C allocation to roots. The common supposition that improved water regime results in less C allocation to roots of woody plants is generally true. However, irrigation does not appear to have an additional effect on fertilization treatments. Thus, while the combination of fertilization and irrigation may improve tree growth and productivity, their combination does not appear to alter C allocation more than fertilization alone. This observation may reflect inherent limits to the degree of plasticity in plants or it may reflect interactions between plant water relations and mineral nutrition.

Table 2. Effects of water (W), nutrients (N) and water plus nutrients (W+N) on distribution of biomass to root systems. expressed as percentage changes relative to **control (stressful)** conditions.

Plant Type	W	N	W+N	Measure	Author(s)
PSME[1] stand	-27	-34	---	BNPP[2]	Gower et al. (1992)
PITA[3] seedlings	-6	-24	-21	k (R:S)[4]	Johnson (1990)
PIEL[5] seedlings	-12	+2	-3	*k* (R:S)	Johnson (1990)
PIRA[6] seedlings	+20	-50	-25	R/TTL[7]	Squire et. al. (1987)
PISY[8] seedlings	-15	-22	-37	BNPP/TNPP[9]	Axelsson (1985)

[1] *Pseudotsuga menziesii*; *Below-ground net primary production; [3] *Pinus* rue&; Allometric coefficient, k, for total root versus total shoot biomass: [5] *Pinus elliottii*; [6] *Pinus radiata*; 'Root biomass as a proportion of total biomass; [8] *Pinus sylvestris*; [9] Below-ground net productivity as a proportion of total net primary productivity

In contrast to rooting of intact plants, it is generally agreed that water-stress of stock plants or cuttings decreases root development (Loach, 1988). Although certainly negative for the rooting of cuttings, mild water-stress in stock plants may have a positive influence on rooting in cuttings collected from such a plant (cf. Rajagopal and Andersen, 1980).

Oxygen

The term "water-stress" is commonly associated with water deficits, but excess water, or flooding, also results in plant stress. One of the principal mechanisms of injury from flooding is through 0, deficit, or hypoxia (Drew and Stolzy, 1991). Removal of O_2 from the root atmosphere results in two significant chemical changes. First, the root is in an energy deficient state due to the low-yielding anaerobic metabolism of glucose (Kramer and Kozlowski, 1979, p. 235). Thus, energy-requiring processes such as nutrient assimilation and growth are decreased. Second, the by-products of anaerobic respiration may be toxic in themselves; [e.g.. ethanol may injure cell membranes (Glinski and Lipiec, 1990, p. 135)]. The net effect on partitioning is a rapid consumption of sugar by inefficient respiration and the potential for accumulation of ethanol as a byproduct of anaerobic decomposition. Few studies have investigated the role of hypoxia on net allocation of C between shoot and root, but C allocation patterns can be inferred to a limited extent from knowledge of root growth responses.

The most commonly observed response of plants to hypoxia is a decrease in root growth which has been shown for a variety of plants [reviewed by Glinski and Lipiec (1990), p. 139]. Although leaf growth can be very sensitive to short-term reductions in soil O_2 (Smit et al., 1989). root growth is usually more sensitive than shoot growth to soil O_2

deficit, leading to a decrease in root-shoot biomass ratio (Kozlowski et al., 1991, p. 321). For example, in hypoxia-resistant woody plants, shoot growth can remain unchanged after 30 days of hypoxic treatments, while root growth and root-shoot ratio may be reduced by more than 30% (Topa and McLeod, 1986). Because root growth is severely limited by O_2 supply, and because growth activity is an important component of sink strength, C allocation to roots is likely to be less under hypoxic conditions than aerobic conditions for most plant species.

Apart from net allocation of C between root and shoot systems, hypoxia may cause allocation to change within the root system. The most notable change is the formation of hyperuophied lenticels and adventitious roots at the soil surface, which may enable partial compensation for the O_2 deficit and impaired functioning of the original root system (Kozlowski et al., 1991, p. 331). Although this response to hypoxia is not evident in all species, and the specific role of hypoxia in the process of adventitious root formation is not yet fully resolved (Haissig, 1986), the phenomenon of adventitious rooting under flooded, hypoxic conditions is clearly of importance as an adaptive mechanism and as a potential key to a basic physiological understanding of the causes of adventitious root formation; both lines of investigation warrant further study.

Other root-oriented adaptations to hypoxia include anatomical changes, such as the formation of structures that improve root access to 0, from above the soil surface. These structures include air channels within the roots (aerenchyma) and air ports on the exterior of the root (lenticels), as well as structures that emerge from the soil and obtain 0, for the roots enduring hypoxic conditions (pneumatophores) (Drew and Stolzy, 1991). The ability of roots to maintain metabolic activity under hypoxic conditions is further assisted by a favorable anaerobic metabolism and by the ability to store carbohydrate reserves to fuel this process (Drew and Stolzy, 1991). Although C allocation to roots is generally reduced under hypoxic conditions, the C costs of inefficient anaerobic metabolism and specialized root structures could conceivably result in greater net C allocation when considered over the growing season in intermittently flooded conditions (for related information, see the chapter by Barlow in this volume).

Light

In general, C allocation to roots of woody plants decreases with decreasing irradiance. This response has been shown from analyses of relative biomass accumulation (Loach, 1970: Kolb and Steiner, 1990a,b) and ^{14}C distribution (Lockhart, 1992). Within this general pattern, however, much complexity exists. Plant species may be more or less plastic in their C allocation patterns in response to light, with variations in successional status and age. For example, greater effects of irradiance on relative biomass accumulation by roots were observed in two-year-old *Quercus* and ***Liriodendron*** seedlings compared with one-year-old seedlings (Kolb and Steiner, 1990a). Few studies have investigated the effects of light quality on C allocation in woody plants, but light quality may also affect C allocation, as evidenced by changes in relative dry matter accumulation in *Pinus* cuttings (Morgan et al., 1983).

In contrast to intact plant root development, decreased irradiance may result in increased rooting in the collected cuttings, although this varies considerably with species (Maynard and Bassuk, 1988; Moe and Andersen, 1988; see the chapter by Howard. and by Murray and coworkers in this volume). For example, *Triplochiton* cuttings taken from shaded plants rooted more when the stock plants were exposed to low rather than high irradiance (Leakey and Storeton-West, 1992). Reports of increased rooting of cuttings grown at low ix-radiance exist, but may be confounded by other environmental factors such as evaporative demand. In a manner similar to intact plants, it appears that better rooting of cuttings is associated with increased irradiance up to a saturation level, due to the importance of carbohydrate supply for developing roots [see Loach (1988), Haissig

(1990)]. The light quality environment of a stock plant may also affect the rooting of cuttings collected. For example, ***Tripbchiron*** cuttings from stock plants grown with a low red:far-red ratio had a better rooting percentage than those from a high red:far-red ratio (Leakey and Storeton-West, 1992). However, light quality effects on rooting cuttings has received little emphasis in the literature.

Temperature

As the net result of enzymatically catalyzed processes, C allocation to a particular sink is likely to decrease when that sink is cooled (cf. Klepper, 1991). In fact, root cooling has been shown to decrease the rate of carbohydrate nanslocation from source leaves [see Bowen (1991)]. As straightforward as this seems, the role of temperature in controlling C allocation in the plant is still uncertain. In a recent review, Bowen (1991) was unable to find any reports of complete C-balance studies that adequately address the effect of temperature on C fluxes in the plant. Particularly uncertain is the effect of temperature on the rate of C loss in exudation. Instead of comprehensive studies, most existing literature focuses on either DW accumulation in roots and shoots, or on dimensional growth, in response to temperature.

In general, root cooling causes shoots to accumulate a greater proportion of biomass than roots, when compared with optimal root temperatures (Bowen, 1991). However, this is a relative increase in shoots. Suboptimal root temperatures actually decrease shoot growth and photosynthesis, even when shoots are growing at optimal temperatures (Vapaavuori et al., 1992). C allocation at supraoptimal root temperatures has received even less attention than that at suboptimal root temperatures. Bowen's recent (1991) review notes that root-shoot biomass ratios are reported to increase or decrease at non-optimal temperatures; some variation is associated with plant age and species. Such generalizations must be made with caution, however, because studies with agricultural crops indicate that relatively complex patterns of root-shoot growth occur in response to temperature when both root and shoot temperature are varied and when plant ontogeny and acclimation are considered (Reddy et al. 1992).

Another root response to temperature, perhaps even more important to plant functioning than C allocation, is root morphology. Root length commonly increases with increasing temperature, with little or no change in root DW (discussed in Bowen, 1991). Thus, as temperature increases, root diameter decreases. Given the importance of root length density (cm root per cm^3 soil) to water and nutrient uptake, the role of temperature in controlling root morphology may be important in causing stress interactions (e.g., cold temperature-nutrient-stress). The similarity between the effects of cold temperatures on root diameter and the observation of larger than normal diameters of roots in adventitiously rooted trees, as previously discussed, suggests that investigations are needed on the physiological controls of root morphology. An additional consideration in the control of rooting is the temperature difference between day and night periods, which may be more important than absolute temperature in affecting certain growth processes (cf. Erwin et al., 1989).

Temperature considerations in adventitious root formation generally agree with intact plant responses in that soil heating to maintain a particular optimum generally improves rooting (Loach, 1988).

TECHNIQUES AND EXPERIMENTAL APPROACHES

Techniques

Two of the more important questions concerning C allocation to roots and shoots are: how much of the plant's C is allocated to roots or shoots? and what are the dynamics of C fluxes within the plant? These questions are especially relevant for the root system, given the inaccessibility of roots for growth and gas exchange measurements. With improvements in the availability of technology for the analysis of radioactive [reviewed by Isebrands and Dickson (1991)] and stable isotopes [reviewed by Ehleringer and Osmond (1991), and Caldwell and Virginia (1991)], such methods can be increasingly relied upon for quantification of C allocation and partitioning in root systems. Isotopes have been used to refine estimates of translocation rates between shoot and roots (Spence et al., 1990) and from roots to the rhizosphere (van Veen et al., 1991); to estimate root turnover and production, N fixation and nutrient acquisition (Caldwell and Virginia, 1991); and to infer patterns of root distribution (Friend et al., 1991). One of the principal advantages of isotopes is that the plant system can be studied in its natural state rather than in an artificial environment, thus avoiding the artifacts associated with most methods of root quantification. At the level of the adventitiously developing root, existing carbon-isotope labelling techniques hold promise for answering many of the persistent questions on the role of stored assimilates in rooting, and about source-sink relations between the shoot and newly developing roots. Particularly, short-term tracing of C within and between roots and shoots may be accomplished with ^{11}C labeling (cf. Schurr and Jahnke, 1991; Spence et al., 1990). and mid- to long-term analysis of C allocation and partitioning may be accomplished by ^{13}C labeling (cf. Cliquet et al. 1990) or ^{14}C labeling (Isebrands and Dickson, 1991).

At the whole-plant level, it has become increasingly apparent that nonstructural C allocation to root systems, including the respiratory costs of growth and maintenance, nutrient uptake, allocation to mycorrhizal fungi and exudation of C from roots into the rhizosphere, may be quite substantial (Buwalda et al., 1992). Recent reviews of methods for quantifying the allocation of C to nonstructural root functions are presented by Lambers et al. (1983). Lambers (1987) and Vogt et al. (1989). An important aspect of this question is the importance of realistic soil environmental conditions for the estimation of respiratory C allocation (cf. Naganawa and Kyuma, 1991). Such techniques for evaluating C fluxes to nonstructural uses may be directly and productively applied to adventitiously developed roots to evaluate their functioning relative to those developing from normal ontogenetic processes.

At the ecosystem or stand level, C allocated to roots is frequently estimated from below-ground net primary production (NPP), which is driven largely by fine root production and estimated from periodic collections of soil cores, careful separation of roots from soil, and analysis of patterns to estimate net C input [reviewed by Vogt and Persson, 1991, and Caldwell and Virgina, 1991; see also the chapter by Dickmann and Hendrick, and by Morita in this volume). Although absorbing or fine roots are the most dynamic and appear to consume the most C, larger, structural roots may serve important storage functions. Quantification of the storage role of the roots of woody plants has also been recently reviewed by Loescher et al. (1990). There is little reason to expect that fully developed stands of adventitiously rooted plants will differ from those of seedling origin in NPP or storage. However, application of these tools in developing stands may provide useful insights, especially in cases where the growth of clonal stands lags behind that of seedlings [e.g., Anderson et al. (1992)].

Another technology for quantifying C allocation to roots in stands is through nondestructive minirhizotron techniques (see the chapter by Dickmann and Hendrick in this volume). Initial efforts in this area relied upon glass or plastic tubes inserted in the soil, with root activity observed with a periscope device and quantified according to root intersections, with scribed lines on the tubes or intersections viewed with an ocular cross-hair (Richards, 1984). The current and most sophisticated technology uses similar tubes with data collected with miniature video cameras, stored on magnetic tape and analyzed with advanced image analysis systems (Brown and Upchurch, 1987; Hendrick and Pregitzer, 1992; see the chapter by Dickmann and Hendrick in this volume). While the magnitude of C consumed by root turnover (root death and subsequent replacement, often with little net change in living root biomass) has received considerable emphasis (Fogel, 1990). new nondestructive techniques using minirhizotron tubes offer great potential for improving estimates of turnover with direct observation of root death and disappearance. Minirhizotron tubes or modifications of this principle might find useful application in the characterization of root development from cuttings in the field. The dynamics and locations of root initiation are usually inferred from destructive harvest, but nondestructive observation of cuttings as they root under field conditions, as could be seen with a rhizotron or minirhizotron, would provide better information on successful rooting characteristics.

In addition to answering specific experimental questions, the output from these root quantification techniques is an important source of data for simulation modelling effons. Root system dynamics is one of the greatest uncertainties in most current growth simulation models. The techniques reviewed above will enable essential root system parameters such as: absolute and relative elongation rate, vertical distribution, root length density, turnover rate and net primary productivity to be determined and incorporated into models. Sensitive techniques will also be essential in refining models to the point that temporal and spatial heterogeneity can be included in modelling root function (cf. Fitter, 1992).

Process Simulation Models

Use of computer simulation models by plant scientists has increased in recent years as the availability and speed of high powered computers has expanded (for related information see the chapter by Rauscher in this volume). Most models are used either as a predictive tool or as a research tool for formulating hypotheses, interpreting results and understanding biochemical and physiological processes. Two types of simulation models are generally recognized, empirical and mechanistic, or process-based. Empirical models describe relationships among variables without reference to the underlying principles; process models are based upon underlying biochemical and physiological processes of the system (Isebrands and Burk, 1992).

There is a multitude of mechanistic process models available for agronomic, herbaceous and forest plants (Thomley, 1976; Whisler et al, 1986; Graham et al., 1985; Isebrands et al., 1990). However, few if any of the models deal adequately with C allocation processes, because the mechanisms of C allocation and partitioning are not fully understood (as discussed previously). Most simulation models allocate C empirically through predetermined allocation coefficients based upon biomass components (Wilson, 1988). One notable exception is ECOPHYS, a physiological process model of juvenile poplar trees growing from hardwood cuttings (Rauscher et al., 1990; see the chapter by Rauscher in this volume), where C is allocated from sources to sinks over the season via dynamic transport coefficients determined from radiotracer studies. However, one of the current limitations to wider applications of the ECOPHYS model results from the lack of knowledge of adventitious root development. For example, we do not understand the factors controlling root initiation and location (i.e., siting) on cuttings, vascular connections between roots and shoots, or the mechanisms of root-shoot feedback in the developing plant. Again, these gaps in knowledge will no doubt require an interdisciplinary team effort, including molecular biology, in order to achieve a solution (Haissig et al., 1992).

In the future, the best use of mechanistic simulation models for understanding adventitious rooting will probably be as an interactive tool for knowledge synthesis in association with experimentation. In parallel modelling and experimentation, process simulation models are valuable for integrating a series of experiments or for testing simpler, empirical simulation models (Isebrands and Burk, 1.992). A good example of this approach is the work of Dick and Dewar (1992). who developed a model of carbohydrate dynamics during adventitious root development in leafy cuttings of *Triplochiton*. They expanded the concepts of Thomley and coworkers concerning balanced root-shoot development (Thomley, 1972, 1976; Johnson and Thomley, 1987) to adventitious rooting in cuttings of woody plants. The processes represented in their model were leaf photosynthesis, starch mobilization, sugar transport and sugar utilization for root growth-a sensitivity analysis was also conducted on model parameters. Although the authors concluded that further parallel experimental work is needed to parameterize and verify their simulation model, this work is a useful new approach for use in conjunction with such experimentation for the eventual understanding of C metabolism during adventitious rooting of cuttings of woody plants.

Woody Plant **Model** Experimental Systems

Throughout this chapter we have emphasized the need for an integrated multidisciplinary research approach to understanding the mechanisms of C metabolism during adventitious rooting of woody plants. In this regard, certain plant materials represent ideal experimental systems for employing this integrated approach (see the chapter by Ernst, and by Riemenschneider in this volume). Without question, the genus *Populus* stands-out among woody plants as a representative with mostly induced or mostly preformed root initials, depending on species. As evidenced by our literature citations, ***Populus*** has been studied in detail by many scientific disciplines at all scales of plant organization. There is a wealth of information on the molecular biology, genetics, biochemistry, anatomy, physiology, propagation and silviculture of the genus. A few of the reasons for selecting ***Populus*** for such a model experimental system are: 1) abundant natural genetic variation in rooting capability, 2) traditional genetic improvement programs that yield pedigreed lines, 3) ease of hybridization and genetic manipulation, 4) molecular genetics research programs (Stettler et al., 1992), 5) fundamental anatomical, biochemical and physiological databases (Isebrands and Dickson, 1991), (6) interdisciplinary research programs (Stettler and Ceulemans, 1993), (7) process simulation models (Isebrands et al., 1990), (8) worldwide economic importance and utilization, and (9) much silvicultural information (Hinckley et al, 1989).

Another candidate for an ideal woody plant experimental system is jack pine (***Pinus banksiana)*** as a representative of a recalcitrant conifer that forms only induced (also termed post-formed) adventitious roots. Jack pine does not have all the "credentials" of ***Populus,*** but it has the advantage of having the most comprehensive fundamental biochemical data base with respect to adventitious rooting of any conifer [see Haissig (1984, 1986, 1988), Haissig et al. (1992)]. In addition, extensive jack pine genetically unique materials exist, and the species is genetically highly variable. Moreover, jack pine flowers at a very young age (i.e., ca. age 3 years) compared to most conifers, and several generations of inbred lines arc available for study. Unfortunately, the companion molecular genetics programs needed for integration with the anatomical and biochemical studies of the controls of adventitious rooting as called for by Haissig et al. (1992) are just beginning.

SYNTHESIS AND FUTURE RESEARCH DIRECTIONS

Synthesis

C allocation in woody plants has been addressed in the fields of plant physiology, ecology. horticulture and forestry. In broad terms, C allocation is controlled by plant and environmental factors. Plant factors include growth patterns (i.e., determinate, indeterminate, semideterminate), and species-specific factors such as those that determine root morphology and the ability to produce adventitious roots. Environmental factors affecting C allocation include but are not limited to nutrients, water, O_2, light and temperature. At a more mechanistic level, C allocation is controlled by source-sink relations. All of these factors cause a shift in allocation by altering the rate at which carbohydrates are loaded, unloaded and consumed by a particular sink. Simple as this may seem, the physiological processes underlying source-sink relations are poorly understood. C allocation is of key importance to adventitiously rooted plant biology because it may help explain poor rooting success and poor field performance, and it may be used to improve the productivity and yield of adventitiously rooted species.

Future Research

Clearly, mote research is needed in all aspects of C allocation in woody plants and especially important is research on C allocation to root systems. We have identified six areas that require urgent attention. The first area involves examining the differences in C allocation between adventitiously rooted plants and those of seedling origin. These differences are most important in species that are difficult to root, because inadequate allocation to roots may offer some explanation for poor field performance. A critical issue is the control of juvenility and maturity in affecting C allocation. Carefully designed and controlled experiments are needed to establish the seasonal C dynamics of seedlings of varying ages in comparison with cuttings of similar sizes.

The second area is in the role of C partitioning in successful adventitious rooting. Much correlative evidence presently exists, including relationships with rooting success and various carbohydrates or environmental factors that are believed to be important because of their effect on carbohydrates. However, other factors may ultimately be more limiting and difficult to control. Thus, it is suggested that researchers attempt to control or at least monitor carbohydrate balance in adventitious rooting experiments. One approach would be to develop optimum carbohydrate balances for cuttings and other vegetative propagules, then use these optima as a baseline in subsequent investigations of environmental and plant effects. Another approach, if carbohydrate allocation or partitioning is believed to be a causal and limiting factor in rooting success, would be to vary carbohydrate balance by, genetic rather than environmental means, and thus remove the other potentially confounding effects of environment on morphogenesis (see the chapter by Riemenschneider in this volume). This could be accomplished, for example, by screening genotypes or mutants for C partitioning patterns. Such standardization would greatly improve the mechanistic understanding of processes affecting adventitious rooting.

The third and perhaps most ambitious area is the mechanistic explanation of C allocation to adventitious roots. While evidence exists for the role of newly developing roots as a sink for carbohydrates, the magnitude to which roots can direct assimilates of leaf *origin is uncertain. Also, resolving the roles (if any) of key enzymes, known to be involved in C partitioning (e.g., SPS) by mediating sink strength, will further a mechanistic understanding of plant and environmental factors that control C allocation to roots. This research direction will necessitate an integrated approach that includes anatomical, biochemical and molecular biological investigations, and will result in basic knowledge useful to all plant scientists.

The fourth area concerns whole-tree C-budgets. Too much of the current information on C allocation is estimated by difference or other indirect means. Experimentation is needed that quantifies structural and functional costs of all major plant organs throughout a growing season. Such research should result in specific C influx and efflux rates for individual tissues that can be used in plant growth simulation models. This approach could also provide useful information in determining relative importance of stored C reserves to rooting and plant establishment for species with different adaptations, growth patterns and life histories.

The fifth area is related to the fourth, but is directed only to the root system. Roots may consume more than one-half of the plant’s C, yet good data on the magnitude and fate of C allocated to the root system are infrequent in the literature. Included under this topic are the C costs of nutrient uptake, symbionts and the potential for “wasteful” respiration and exudation. For such information to be useful to simulation modelling efforts, more information on root dynamics is also needed. This effort will include variation in C allocation and physiological activity over spatial and temporal scales. Much of the inaccuracy of current simulation models results from the overuse of physiological parameters collected from a single time during the growing season.

In the sixth and final area, more whole-plant simulation modelling efforts are needed in conjunction with whole-plant C allocation experimentation. Such efforts will provide guidance in the processes that are most important for study, and in the appropriate level for examination of the processes. Simulation models can thus help identify gaps in knowledge and provide feedback to experimentation. A successful illustration of this approach to solving problems associated with adventitious rooting is provided by Dick and Dewar (1992).

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